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RELATION D'AUTO-ÉCLAIRCISSEMENT ET PRODUCTION CHEZ LES POPULATIONS D'OMBLE DE FONTAINE, *SALVELINUS FONTINALIS*, EN SYMPATRIE AVEC LES JUVÉNILES DU SAUMON ATLANTIQUE, *SALMO SALAR*.

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RÉSUMÉ

À l'intérieur de population limitée par l'espace ou la nourriture disponible, une relation limitante et dynamique appelé auto-éclaircissement (*self-thinning*), réfère à une diminution de la densité de population d'une cohorte à capacité de soutien, résultant de la compétition au fur et à mesure que les individus à l'intérieur de la cohorte augmentent en taille. Les paramètres (la pente et l'ordonnée à l'origine) de la relation d'auto-éclaircissement permettent une description succincte de la façon dont la densité et la biomasse varient simultanément à l'intérieur des populations animales sédentaires. Nous avons examiné si dans les populations d'omble de fontaine, *Salvelinus fontinalis*, la relation d'auto-éclaircissement (1) avait une pente de -0,75 prédite en se basant sur des considérations métaboliques et (2) était influencée par le type d'habitat et la densité d'un compétiteur potentiel, le saumon atlantique, *Salmo salar*. Durant les étés de 1993 à 1995, nous avons obtenu des estimés de densité et de biomasse par la pêche électrique dans trois sites différents (en ruisseau) à l'intérieur desquels six sections furent échantillonnées (3 fosses et 3 rapides adjacents deux à deux). Les paramètres d'auto-éclaircissement ont été estimés pour chaque section et chaque période d'échantillonnage et en combinant toutes les années d'échantillonnages, par une régression de type II (axe majeur). Dans des conditions près de l'allopatrie (très faible densité de saumons) dans les rapides, la pente moyenne de la relation d'auto-éclaircissement n'était pas significativement différente de -0,90 (métabolisme des salmonidés), mais les pentes et les ordonnées à l'origine différaient de celles en situation de sympatrie et entre les deux types d'habitat (fosse et rapide). Une analyse combinée de ces

deux paramètres par MANCOVA indiquait une influence marquée du type d'habitat et de la densité de saumons atlantique sur la relation d'auto-éclaircissement. La profitabilité reliée à l'habitat chez les ombles semble plus élevée dans les fosses que dans les rapides et diminue avec l'augmentation des densités de saumons. Les résultats démontrent la nécessité de considérer les effets de l'habitat et des compétiteurs dans l'analyse de l'auto-éclaircissement dans les populations animales. Par ailleurs, les approches conventionnelles permettant d'estimer la production annuelle, requièrent souvent l'échantillonnage des populations à deux ou plusieurs occasions. Plusieurs études sur les salmonidés en ruisseau démontrent que la relation d'auto-éclaircissement décrit souvent adéquatement la trajectoire temporelle du déclin dans le nombre des individus à l'intérieur d'une cohorte en relation avec l'augmentation de la masse individuelle moyenne. Cette relation produit donc une vue instantanée de la production d'une population. Nous avons utilisé la méthode numérique de Ricker et une nouvelle méthode basée sur l'intégration de l'aire sous la courbe de la relation d'auto-éclaircissement pour calculer la production annuelle de l'omble de fontaine dans trois sites en ruisseau. Les estimés de production obtenus par les deux méthodes étaient bien corrélés et étaient influencés de la même façon par différentes sources de variation: la variabilité temporelle, les différences entre les habitats et l'effet de la présence de juvéniles du saumon atlantique. Dans les populations de salmonidés qui se conforment à la relation d'auto-éclaircissement, la production annuelle peut être estimée à partir d'un échantillonnage ponctuel par cette relation. Parce qu'elle réduit l'effort d'échantillonnage, cette approche pourrait fournir une alternative utile aux méthodes conventionnelles qui requièrent un échantillonnage répété, particulièrement pour des suivis comparatifs sur des sites multiples dispersés sur un grand nombre de cours d'eau.

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AVANT-PROPOS

C. Dussault apparaît comme coauteur dans les deux articles qui se retrouvent dans ce mémoire. Ceci reflète son implication dans le cadre de son projet de maîtrise, dans la prise de données de densité et de poids des poissons pour l'année 1994. Le plan d'échantillonnage et les travaux sur le terrain pour l'année 1995, ainsi que l'analyse des données et la rédaction du mémoire présent, ont été réalisés entièrement par S. Trépanier, sous la supervision de M.A. Rodríguez.

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INTRODUCTION

Le concept premier qui est à la base de la démarche de ce projet de recherche était la relation d'auto-éclaircissement, "self-thinning" dans la littérature anglaise. Ce processus survient à l'intérieur de population limitée par l'espace ou la nourriture disponible et réfère à une diminution de la densité de population d'une cohorte à capacité de soutien, résultant de la compétition au fur et à mesure que les individus de la cohorte augmentent en taille. (Figure 1).

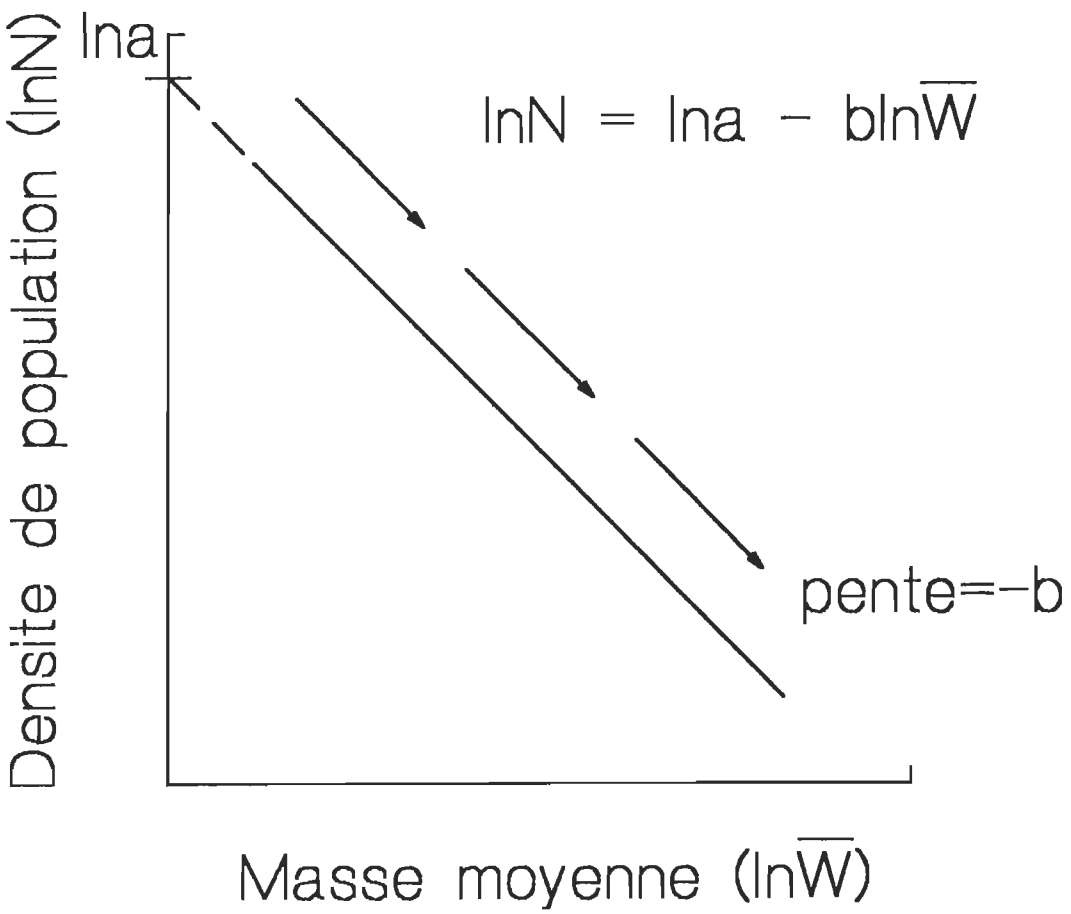

Figure 1. Représentation schématique de la relation d'auto-éclaircissement entre la densité et la masse moyenne des individus d'une cohorte.

Ce processus a d'abord été démontré chez les végétaux où la pente de la relation semblait être constante et égale à -3/2. Étant donné la constance de cette relation, certains écologistes végétaux ont appelé cette relation "la règle de -3/2" (Yoda et al. 1963, White 1981). Par la suite, plusieurs auteurs ont remis en question la constance de ce phénomène en démontrant plusieurs variations dans les paramètres de la relation d'auto-éclaircissement (Weller 1987; Lonsdale 1990).

D'autres études ont par la suite étendu le domaine d'application de la relation d'auto-éclaircissement en vérifiant celle-ci chez une population de criquets (*Chorthippus brunneus*; Begon et al. 1986) et chez certaines populations de mollusques (Hughes & Griffiths 1988; Fréchette & Lefaivre 1990, 1996; Marquet et al. 1990). Plus récemment, l'existence de cette relation dynamique a été démontrée chez des populations de salmonidés (Grant 1993; Elliott 1993; Bohlin et al. 1994). Ainsi, la base théorique principale servant à expliquer le fonctionnement de la relation d'auto-éclaircissement est la suivante: puisque le taux métabolique des animaux (M) est souvent proportionnel à la masse individuel (W) élevée à la puissance 0,75 (Kleiber 1961, Peters 1983), le taux métabolique moyen à l'intérieur d'une population devrait être proportionnel à la masse moyenne élevée à la même puissance. Le taux métabolique moyen devrait aussi être proportionnel à la quantité de nourriture consommée par individu, F / N (Elliott 1993), où F est la quantité totale de nourriture consommée et N est la densité de population. Ainsi:

$$\frac{F}{N} \alpha \overline{W}^{0,75} \qquad (1)$$

ou

$$N \alpha \left(\frac{F}{\overline{W}} \right)^{0,75} \quad (2)$$

et si F est constant, alors:

$$N \alpha \overline{W}^{-0,75} \quad (3)$$

ou

$$\ln N = \ln a - 0,75 \ln \overline{W} \quad (4)$$

où a représente la capacité de soutien du milieu et b représente le rapport mortalité/croissance (m / g ; Bohlin et al. 1994). La constance de F pendant la croissance d'une cohorte a souvent été contestée (Begon et al. 1986, Elliott 1993). Par contre, dans le cas des salmonidés en ruisseau, on pourrait s'attendre à ce que F soit constant puisque la source d'énergie ou de nourriture qu'est la dérive (invertébrés circulant dans la colonne d'eau) est renouvelée constamment, ne s'accumule pas et n'est pas affectée par la population elle-même (Allan 1982, Grant 1993).

L'équation (4) représente la relation d'auto-éclaircissement tel que décrit sur la figure 1 avec une pente de -0,75. Dans le même sens, Bohlin et al. (1994) ont utilisé l'approche de l'hypothèse d'équivalence énergétique, qui stipule que la quantité d'énergie que chaque espèce utilise par unité de surface de son habitat est indépendante de sa taille corporelle (Damuth 1987, Nee et al. 1991). Cette énergie pouvant être reliée à la quantité de nourriture totale consommée utilisée par Elliott (1993). Par contre, Bohlin et al. (1994) ont plutôt suggéré que le facteur qui relie le métabolisme à la taille corporelle chez les salmonidés pourrait être différent de 0,75, qui semble plus approprié pour les animaux homéothermes, alors que chez les poissons on retrouverait un facteur plus près de 0,90 (Glass 1969). Par

contre, si on considère que la densité des populations de salmonidés est plutôt reliée à la relation entre la taille des territoires et la taille corporelle, on obtient une pente de -0,86 (Grant & Kramer 1990). Dans leur étude, Grant & Kramer (1990) ont montré que si $\log_{10}$ densité = 2,83 - 2,61 $\log_{10}$ longueur à la fourche, et que $\log_{10}$ masse = 3,03 $\log_{10}$ longueur à la fourche - 1,93, alors le $\log_{10}$ masse = 1,35 - 1,16 $\log_{10}$ densité, donnant une pente de -0.86 (-1/1.16; basé sur l'équation 4 où la densité est reliée à la masse moyenne). Par ailleurs, si l'habitat peut supporter une biomasse (B) constante indépendamment de la taille des individus dans une cohorte, on pourrait s'attendre à avoir une pente de -1,00 durant l'auto-éclaircissement (Peters 1983, Begon et al. 1986, Grant 1993). On obtiendrait alors:

$$\ln N = \ln a - 1{,}00 \ln \overline{W} \tag{5}$$

$$\ln a = \ln N\overline{W} \tag{6}$$

$$a = N\overline{W} = B \tag{7}$$

La relation d'auto-éclaircissement est donc une relation dynamique qui pourrait être influencée par plusieurs facteurs. Dans les études antérieures, une seule espèce était considérée (situation allopatrique) à l'intérieur d'habitats relativement homogènes (Grant 1993, Elliott 1993, Bohlin et al. 1994). Ainsi, les insectes dérivants qui sont la source principale de nourriture pour les juvéniles du saumon atlantique, *S. salar*, et pour l'omble de fontaine , *S. fontinalis*, en ruisseau (Wankowski & Thorpe 1979, Williams 1981, Randall 1982), pourraient avoir une dynamique différente entre divers types d'habitats. La vitesse du courant et la profondeur moyenne diffèrent de façon marquées entre les fosses et les rapides. Ces différences peuvent influencer le taux d'arrivée des proies dans un secteur donné

(Everest & Chapman 1972, Wankowski & Thorpe 1979), l'accumulation de proies qui se retrouvent au fond des fosses (McLay 1970), le coût énergétique des tentatives d'alimentation (Cole & Noakes 1980, McNicol & Noakes 1984), du maintien d'une position dans le courant (Arnold et al. 1991) et de la défense d'un territoire d'alimentation (McNicol & Noakes 1981, McNicol & Noakes 1984, Grant & Noakes 1988). Considérant toutes ces différences, on pourrait s'attendre à retrouver des différences dans les taux de croissance ou de mortalité, ainsi que des différences dans la quantité totale de nourriture consommée entre les deux habitats pour les populations d'omble de fontaine, et par conséquent, des différences entre les pentes et ordonnées à l'origine de la relation d'auto-éclaircissement.

De plus, des différences dans les densités de compétiteurs potentiels pourraient aussi influencer les paramètres de la relation d'auto-éclaircissement. Les jeunes salmonidés en ruisseaux défendent souvent des territoires d'alimentation (Latta 1969, Dill et al. 1981, McNicol et al. 1985), peu après l'émergence du gravier (Noakes 1980). Les juvéniles du saumon atlantique et les ombles semblent être abondants dans les zones peu profondes à forts courants au début de l'été (Keenleyside 1962, Gibson et al. 1993), mais plus tard dans la saison, lorsque la nourriture devient plus rare, les saumons peuvent déplacer les ombles des rapides vers les fosses (Gibson 1973, Gibson et al. 1993). L'omble de fontaine émerge 2 à 3 semaines avant les saumons (Randall 1982) et ainsi, ont un poids plus important à n'importe quelle période durant l'été, leur donnant un avantage relié à la taille dans les fosses sur les juvéniles de saumons, plus agressifs (Keenleyside 1962, Gibson 1993, Randall 1982). Les saumons, par contre, ont des nageoires pectorales plus grosses qui leurs permettent de rester en contact avec le substrat et ont une flottabilité plus faible (Saunders

1965), leurs donnant avec l'agressivité, plus de succès dans les rapides, lors d'interactions interspécifiques (Gibson 1973, Randall 1982). Dans une situation de sympatrie, lorsque le taux d'arrivée en proies est plus important dans les rapides, les juvéniles du saumon atlantique pourraient affecter l'alimentation de l'omble de fontaine par exploitation des ressources alimentaires disponibles ou par interférence, lorsqu'ils tentent de se nourrir. Cette dominance comportementale des juvéniles de saumon atlantique sur l'omble pourrait changer la pente, b, en influençant la mortalité ou la croissance (Gibson et al. 1993) et l'ordonnée à l'origine de la relation d'auto-éclaircissement, en réduisant la quantité totale de nourriture consommée (Bohlin et al. 1994).

Puisque la relation d'auto-éclaircissement représente les changements dynamiques (à l'intérieur d'une cohorte) de la croissance et de la densité d'une population, elle pourrait être utilisée pour caractériser la dynamique d'une population, plus particulièrement afin de suivre la production d'un ruisseau dans le temps ou dans l'espace estimée sur plusieurs sites. La production est définie comme la quantité de tissus élaborée dans un intervalle de temps, incluant ceux formés par les individus qui ne survivent pas jusqu'à la fin de l'intervalle (Ivlev 1966). La production est souvent considérée comme une des mesures les plus utiles pour représenter la dynamique ainsi que la performance environnementale d'une population, puisqu'elle fait intervenir deux des paramètres dynamiques d'une population, soit le nombre d'individus ainsi que leur taux de croissance (LeCren 1969, Hunt 1974, Waters 1977, 1992). Les méthodes souvent utilisées pour calculer la production annuelle incluent des estimations numériques basées sur des modèles spécifiques de croissance et de mortalité (Ricker 1946), et des méthodes graphiques (Allen 1951).

La méthode numérique de Ricker utilise des modèles exponentiels de croissance et de mortalité et se calcule suivant la formule $P = G\overline{B}\Delta t$ où P = la production; G = le taux instantané de croissance; $\overline{B}$ = la biomasse moyenne durant Δt; et Δt = l'intervalle de temps couvrant l'estimation de la production (Chapman 1978). Dans la méthode de Allen (1951), les estimés de production sont obtenus en reliant graphiquement le nombre d'individus (N) dans la population en fonction de la masse moyenne ($\overline{W}$) des individus à des moments successifs. Ainsi, en calculant l'aire sous la courbe qui relie l'ensemble des points, on obtient un estimé de la production dans un intervalle de temps donné. Par ailleurs, pour les populations qui suivent la relation d'auto-éclaircissement, la production annuelle pourrait être estimée en intégrant afin d'obtenir l'aire sous la courbe de la façon suivante:

$$P = k\int_{\overline{W}_i}^{\overline{W}_f} \overline{W}^{-b}\, dw \tag{8}$$

$$P = \frac{k}{1-b}\left(\overline{W}_f{}^{1-b} - \overline{W}_i{}^{1-b}\right) \tag{9}$$

où P est l'évaluation de la production annuelle; k est l'ordonnée à l'origine dans la relation d'auto-éclaircissement; b est la pente de la relation d'auto-éclaircissement; $\overline{W}_f$ est la masse moyenne des individus pour la classe d'âge la plus vieille incluse dans la relation d'auto-éclaircissement et $\overline{W}_i$ est la masse moyenne pour la classe d'âge la plus jeune. Ainsi, dans des situations où la relation d'auto-éclaircissement décrit fidèlement la croissance et la mortalité, il serait possible d'obtenir des estimés de production annuelle en échantillonnant les densités de poissons dans un ruisseau seulement une fois durant l'été.

Plusieurs auteurs ont considéré que dans la méthode de Ricker, on doit échantillonner une population plusieurs fois dans une année pour obtenir des estimés de production annuelle adéquats (Waters 1977), jusqu'à quatre fois par année (Randall 1981) et même à tous les mois afin d'avoir des estimés de croissance et de mortalité qui soient exponentielles (Chapman 1978). Dans le cas de la méthode de Allen, on doit également avoir les intervalles de temps les plus courts possibles afin d'obtenir une courbe représentative du déclin réel des densités avec l'augmentation de la masse moyenne (Chapman 1978). Par contre, si on considère a priori que les populations sont en équilibre d'année en année, le calcul de l'aire sous la courbe reliant les points des différentes classes d'âge d'une population à un moment donné, pourrait également donné un estimé de production comparable à celui obtenu par l'aire sous la courbe de la relation d'auto-éclaircissement (Cooper & Scherer 1967, O'Connor & Power 1976, Chapman 1978). Cependant, la courbe d'Allen ne suppose aucun modèle de croissance ou de mortalité, ajustant la courbe aux données de nombre et de poids moyens disponibles.

Étant donné le lien entre la méthode numérique de Ricker et la méthode basée sur la relation d'auto-éclaircissement, certaines conditions environnementales pourraient influencer de la même façon les deux méthodes dans le calcul des estimés de production (voir description des effets possibles de divers types d'habitats et des densités de compétiteurs sur la croissance et la mortalité aux pages 4-6).

Les objectifs de cette étude étaient donc de vérifier (1) si la relation d'auto-éclaircissement avait une pente de -0,75 chez les populations d'omble de fontaine, (2) si le

type d'habitat (fosse et rapide) et la densité d'un compétiteur potentiel, le saumon atlantique, pouvaient avoir une influence sur les paramètres de cette relation; (3) si la relation d'auto-éclaircissement pouvait être utilisée pour calculer la productivité d'un ruisseau au même titre que les méthodes couramment utilisées dans le calcul de la production annuelle et (4) si les estimés de production calculés par ces deux méthodes étaient influencés par le type d'habitat et la densité de compétiteurs.

CHAPITRE I

SELF-THINNING IN BROOK TROUT, *SALVELINUS FONTINALIS*, POPULATIONS IN SYMPATRY WITH JUVENILE ATLANTIC SALMON, *SALMO SALAR*: EFFECTS OF HABITAT TYPE AND DENSITY OF POTENTIAL COMPETITORS.

Self-thinning in brook trout, *Salvelinus fontinalis*, populations in sympatry with Atlantic salmon, *Salmo salar*: effects of habitat type and density of potential competitors

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ABSTRACT

In populations limited by spatial or food resources, the limiting dynamic relation describing the decrease in numbers of a cohort that results from competition as individuals in the cohort increase in size, is termed self-thinning. The slope and intercept of the relation between ln(density) and ln(mean individual mass) can provide a succinct and informative description of self-thinning in sedentary animal populations. We examined whether in brook trout, *Salvelinus fontinalis*, populations the self-thinning relation (1) had the slope of -0.90 predicted by a metabolic hypothesis that assumes constant energy use in salmonid populations, and (2) was influenced by habitat type and the population density of a potential competitor, the Atlantic salmon, *Salmo salar*. In the summers of 1993-1995, we estimated fish density and individual mass by electrofishing in three pool and three riffle sections at each of three stream sites. Self-thinning parameters were estimated for each section and each sampling period separately (all year periods combined) by model II (major axis) regression. Under near-allopatric conditions in riffles, the mean self-thinning slope did not differ significantly from -0.90, but the slope and the intercept differed from those in sympatry with salmon. A joint analysis of the slope and intercept by MANCOVA indicated a marked influence of habitat type and salmon densities on the self-thinning relation. Habitat suitability for trout appeared to be higher in pools than in riffles and to decrease with increase in salmon densities. The results highlight the need for considering habitat and density of potential competitors in analyses of self-thinning in animal populations.

Key words: interspecific competition, energy equivalence hypothesis, stream salmonids, allometry, metabolism, energy flow, Quebec

Introduction

In populations limited by spatial or food resources, the limiting dynamic relation describing the decrease in numbers of a cohort that results from competition as individuals in the cohort increase in size, is termed self-thinning (Grant 1993, Bohlin et al. 1994). The process can be described by the temporal trajectory of density-dependent decline of number of individuals in a cohort in relation to increase in mean individual weight. The applicability of the self-thinning relation to populations of mobile animals has received much attention in recent years (crickets: Begon et al. 1986; salmonid fish: Elliott 1993, Grant 1993, Bohlin et al. 1994). Given that the density of stream-dwelling salmonids may be limited by food availability (Mason and Chapman 1965, Slaney and Northcote 1974, Dill et al. 1981), and that metabolic rate, M, is related allometrically to body weight, W, in animals as $M = kW^b$ (Peters 1983, Damuth 1987), the total energy passing through a population, F, can be related to population density, N, and mean metabolic rate, $k\overline{W}^b$ as (Elliott 1993, Bohlin et al. 1994):

$$F = NM \tag{1}$$

so that

$$F = Nk\overline{W}^b \tag{2}$$

or

$$\ln N = \ln(F / k) - b \ln \overline{W} \qquad (3)$$

Eq. (3) describes the self-thinning process. The equation intercept, $\ln(F / k)$, reflects carrying capacity of the habitat, and the slope, b, represents the ratio of specific or per capita mortality to growth rates (m / g) in this habitat (Bohlin et al. 1994). However, the assumption that F is constant has been questioned (Begon et al. 1986). Elliott (1984) argued that because of the year-to-year consistency of density-dependent mortality for different year-classes in his study, neither space nor food availability changed markedly between years. Likewise, Bohlin et al. (1994) interpreted the results of their self-thinning study as resulting from competition between individuals over energy resources that tend to be constant from year to year.

Various hypotheses concerning the value of b, the slope of the self-thinning relation, have appeared in the literature. If the environment can support a constant biomass regardless of the mean mass of individuals in the cohort, a slope of -1.0 is expected during self-thinning (the biomass equivalence hypothesis; Peters 1983, Begon et al. 1986, Grant 1993). The energetic equivalence hypothesis (Damuth 1987; Nee et al. 1991; Marquet et al. 1995) assumes that F, the total energy used by a population per unit area, is constant. Given that metabolic rate in animals is generally proportional to individual weight to the power of 0.75 (Kleiber 1961, Peters 1983), total energy use by the population should be proportional to (mean weight)$^{0.75}$ (eq. 2), and thus the slope of the self-thinning relation should be -0.75 (eq.3). Elliott (1993) showed that in brown trout, *Salmo trutta*, the slope of self-thinning relation for 23 year-classes was not significantly different from -0.75. Grant (1993), using published data, found that three of four studies were consistent with a self-thinning line with slope -0.75. However, Bohlin et al. (1994) stressed that the mean metabolic rate for

salmonids was closer to 0.90 than to the value of 0.75 (Glass 1969) Their estimate for the self-thinning slope (-0.98; 95% confidence interval -0.84 to -1.13) for three stream salmonids in southern Sweden, was not significantly different from the prediction of -0.90 derived from the energetic equivalence hypothesis. Their reanalysis of data for juvenile Atlantic salmon in Shelligan Burn, Scotland (Egglishaw and Shackley 1977) yielded an estimate of -0.91 for the slope of self-thinning relation (Bohlin et al. 1994). A reanalysis of the relation between territory size and body size for stream salmonids (Grant and Kramer 1990) yielded a self-thinning slope of -0.86 (Bohlin et al. 1994).

Drifting invertebrates are the primary food source for juvenile Atlantic salmon, *S. salar* and brook trout, *S. fontinalis* in streams (Wankowski and Thorpe 1979, Williams 1981, Randall 1982). Differences in water velocity and depth between pools and riffles may influence prey delivery rate (Everest and Chapman 1972, Wankowski and Thorpe 1979), loss of prey by sinking (McLay 1970), as well as the energetic costs of feeding attempts (Cole and Noakes 1980, McNicol and Noakes 1984), of holding position (Arnold et al. 1991), and of territorial defense (McNicol and Noakes 1981, McNicol and Noakes 1984, Grant and Noakes 1988). These differences could lead to differences in total food supply, growth and mortality rates between the two habitats, thus changing the intercept and slope of the self-thinning relation.

Differences in density of competitors also can be expected to modify the intercept and slope of the self-thinning relation. Studies of self-thinning in salmonid fish deal mostly or exclusively with species in allopatric situations (Grant and Kramer 1990; Elliott 1993; Grant 1993; Bohlin et al. 1994). Young salmonids in streams commonly defend feeding territories (Latta 1969, Dill et al. 1981, McNicol et al. 1985), and begin to do so soon after emergence

(Noakes 1980). In sympatry, brook trout and Atlantic salmon can use shallow, fast-flowing waters simultaneously early in summer (Keenleyside 1962, Gibson et al. 1993); later in summer, when food becomes more sparse, salmon can displace trout from riffles to pools (Gibson 1973, Gibson et al. 1993). Brook trout emerge from the gravel about 2-3 weeks earlier than salmon (Randall 1982) and therefore are larger than salmon of similar age in summer, possibly giving trout a size advantage in pools over the more aggressive juvenile salmon (Keenleyside 1962, Griffith 1972, Randall 1982). Salmon have larger pectoral fins which allow them to stay in contact with the substrate and are less buoyant than trout (Saunders, 1965), which presumably enables them to exploit riffles more efficiently than trout (Gibson 1973, Randall 1982). Atlantic salmon may affect brook trout foraging by exploitation of food resources or by behavioral interference. Competitive effects of juvenile salmon on brook trout could change the self-thinning slope for trout by influencing mortality and growth (Kennedy and Strange 1986, Gibson et al. 1993), and could also reduce the intercept of the self-thinning relation by reducing total food consumption (Bohlin et al. 1994).

The objectives of this study were to examine whether in stream-dwelling brook trout the self-thinning relation (1) had the slope of -0.90 predicted by a metabolic hypothesis that assumes constant energy use in salmonid populations, and (2) was influenced by habitat type and the density of a potential competitor, the Atlantic salmon.

Materials and methods

The three study sites, Chandler Creek (48º37' N, 67º06' W), North Gunn Creek (48º32' N, 67º07' W), and South Gunn Creek (48º32' N, 67º06' W) are located in the Matapedia Valley, eastern Quebec, Canada. Brook trout and Atlantic salmon are the dominant species at the study sites; slimy sculpin, *Cottus cognatus*, and longnose dace, *Rhinichthys cataractae*, are present also at low densities in Chandler Creek. Salmon were nearly absent in North Gunn Creek (table 1), resulting from few fish that can migrate upstream between South Gunn Creek and North Gunn Creek sites. North Gunn Creek study sites will be therein described as near allopatry, and South Gunn Creek and Chandler Creek sites as sympatry sites. At each site, fish were sampled in three short stream stretches consisting each of a pool section adjacent to a riffle section (mean section area ± SD = 67.7 ± 31.6 m^2). The distances between pairs were of 14 and 225 meters in Chandler Creek, 37 and 14 meters in North Gunn Creek, and 29 and 33 meters in South Gunn Creek. Samples were collected three times during the summer (June 7-17, July 5-24, August 2-20) in 1993, 1994, and 1995. Each section was closed with modified seine net (6 mm mesh size) and fish were collected by electrofishing with a backpack shocker (Smith-Root model 15-C) in an upstream direction (3 to 6 passes). Fish were anesthetized with MS-222, weighted to the nearest centigram, and measured to the nearest millimeter. Fish densities (numbers per 100 m^2) were estimated separately for each species and age-class (removal method, Rexstead and Burnham 1991). Fish were assigned to age-classes 0+, 1+, and ≥ 2+ on the basis of length-frequency distributions, verified by examination of scales (Lacroix 1989).

The geometric means of individual weight in each section was calculated separately for each age-class. Density was transformed as $\ln(X + 1)$ and mean mass was transformed as $\ln X$. The slope and intercept of the self-thinning relation were estimated by model II (major axis) regression, which is more appropriate for allometric relations than ordinary least-squares regression (Ricker 1973 1984, McArdle 1988, LaBarbera 1989). Reduced major axis regression produces a line that minimizes the sum of the products of vertical and horizontal deviations of points from the line. However, it does not consider any information about the covariance between Y and X when calculating the slope. We did not use reduced major axis regression because it can yield nonsensical results, such as a large non-zero slope between two variates that are uncorrelated (Harvey and Pagel 1991). We performed 18 regressions, one for each of the 18 sections, for each sampling period separately. Data for each section therefore encompassed variation among years and age-classes. To account for possible covariation in the slope and intercept of the self-thinning relations, we analyzed these two parameters jointly by MANCOVA (Wilkinson 1990), to evaluate the effects of salmon density and habitat type.

Results

The slopes and intercepts for self-thinning lines in brook trout populations differed considerably among study sites and between sampling periods, both in near allopatry and sympatry with Atlantic salmon (Fig. 1, Table 2). Intercepts of the self-thinning lines were higher and slopes less steep in pool habitats than riffle habitats (Fig. 2, Table 2). Intercepts were lower and slopes were less steep in sympatry with salmon than in near allopatry (Fig. 2,

Table 2). In riffles, near-allopatric populations had a mean slope not significantly different from -0.90 in July and August (Table 2).

Both habitat type and salmon density had a significant effect on the slope and intercept of self-thinning lines (Table 3). The interaction of these two variables was not significant. We used MANCOVA results to obtain two new variables, linear combinations of the slope and intercept that specified directions along which effects of habitat type and of salmon densities were strongest (Fig. 2). We used the variables defined by the linear combinations to calculate expected slopes and intercepts for each habitat type at mean salmon density (Fig. 3). We also obtained expected slopes and intercepts (average across habitats) for low salmon densities (mean for North Gunn Creek), medium (overall mean) and high salmon densities (mean for Chandler Creek) (Fig. 3). Summary self-thinning lines (fig. 3) showed that slopes were steeper and intercepts lower in riffles, i.e., that inter-habitat differences in numerical abundance were greater for larger brook trout. This graphical pattern reflects increased use of pools as individuals grow older and longer. Increases in salmon density made slopes less steep and reduced the value of intercepts (Fig. 3), implying that the numerical density of younger, smaller trout declined more strongly than that of older trout with increases in salmon density. This result is consistent with intersite differences in total salmon density and densities of 0+ trout (Table 1).

Discussion

In agreement with other studies (Grant and Kramer 1990, Bohlin et al. 1994), the average slope for riffles in near allopatry did not differ significantly from that predicted by metabolic considerations, b = -0.90. Grant and Kramer (1990), examining limitation of

density by territory size in salmonids, argued that this hypothesis possibly would not apply to deeper habitats such as pools. Higher areal densities can occur in pools because fish distribution is not strongly restricted along the vertical dimension as occurs in shallow habitats. Our results suggest that although in riffle habitats the self-thinning slope is near -0.90 in the absence of potential interspecific competitors, the slope and intercept may vary in other habitats or in the presence of interspecific competitors.

Riffles had steeper slopes than pools. In a closed system (no migration), this result would imply that the mortality/growth ratio was lower for pools (Bohlin et al. 1994). Because our study system is open, mortality cannot be distinguished from permanent emigration. The steeper slopes in riffles could thus be due primarily to movement of larger trout from riffles to pools (Gibson et al. 1993; Heggenes et al. 1995). The positive slopes observed at high salmon densities (Fig. 2) cannot result from self-thinning which is associated always with decline in density through time. Instead, they probably result from a "subsidy" of larger fish from nearby riffles, coupled with a decline in density of younger brook trout caused by competition with juvenile salmon. In five Swedish streams, the slope of the self-thinning relation had a mean value of -0.98, but intercepts and slopes varied widely between sites and had a positive slope in some sites (Bohlin et al. 1994). They interpreted the occurrence of self-thinning as a result of competition for energy resources that tend to be constant from year to year within sites, with mortality and growth constant. They suggested that in sites with positive slopes, low recruitment is compensated by increase in growth or decrease of mortality for fish remaining at the site, possibly combined with immigration from adjacent areas (Bohlin et al. 1994).

Pools had higher intercepts than riffles, reflecting higher carrying capacity or total food availability in the former. Available habitat volume is higher in pools, possibly allowing more trout territories to be maintained in this habitat (Grant and Kramer 1990). Brook trout may have access to a larger food base in pools than in riffles, because prey items sink to the bottom more readily at the lower velocities characteristic of pools (McLay 1970). Brook trout in pools also tend to school instead of defending territories, possibly allowing for more fish to be maintained per unit area than in riffles (Keenleyside 1962; Gibson 1978). Thus, in sympatry with juveniles of Atlantic salmon, pools seemed to be better habitat for brook trout than riffles, a finding that agrees with earlier studies (Keenleyside 1962, Gibson 1966, Gibson 1973, Rodríguez 1995).

Increases in the density of Atlantic salmon lowered the intercept and flattened the slope of the thinning line. This pattern reflected an overall reduction of trout density across all age-classes, with stronger negative effects on smaller, younger trout. High densities of Atlantic salmon parr have been shown to influence growth and survival of brown trout fry (Kennedy and Strange 1986). Atlantic salmon may have similar negative effects on the number of yearling brook trout in some habitats, thus reducing recruitment to older groups (Gibson and Myers 1986). Earlier studies demonstrated that yearling brook trout are the age-class most severely affected by the presence of juvenile Atlantic salmon (Gibson 1973, Gibson et al. 1993). In the study of Gibson (1973), the proportion of trout older than underyearlings went from 70 and 73% in two sections where salmon were absent or sparse to 19 and 29% in two sections where salmon were abundant. The present results support those earlier findings. In near allopatric sites (North Gunn Creek), brook trout in the age-class 0+ comprised 74.3 % of the total density of trout, but in sympatric sites this percentage

declined, to 59.8% in South Gunn Creek, and 32.7% in Chandler Creek, where mean salmon densities were 23.9 and 24.3 fish per 100 m^2, respectively.

In this study, the self-thinning relation provided a simple and interpretable representation of brook trout population dynamics, integrating habitat effects and size-dependent interactions. The self-thinning relation may generally provide a suitable basis for temporal and spatial comparisons of population dynamics within and among trout streams (Elliott 1993, Bohlin et al. 1994), but this potential still requires verification. Future studies of the self-thinning relation should take into account the potential effects of habitat type and interspecific competitors.

Acknowledgments

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References

(Voir pages 61-71 à la fin du document pour les références de cet article)

Table 1. Density and capture probability for population estimates, by species. D = density (numbers per $100m^2$), p = probability of capture estimated by the removal method (n = 4 to 27 sections). Current velocity and water depth (mean ± SD) are also given.

		Chandler Creek				North Gunn Creek				South Gunn Creek			
		Pool		Riffle		Pool		Riffle		Pool		Riffle	
Species	Age	D	p	D	p	D	p	D	p	D	p	D	p
Brook	0+	4.3	0.83	2.2	0.74	71.7	0.60	59.4	0.53	40.1	0.60	21.1	0.60
trout	1+	8.7	0.77	3.0	0.78	27.8	0.72	7.1	0.72	16.3	0.52	7.4	0.61
	≥2+	6.9	0.91	0.4	0.90	17.9	0.82	2.5	0.88	13.3	0.62	3.1	0.78
	Total	19.9	-	5.6	-	117.4	-	69.0	-	69.7	-	31.6	-
Atlantic	0+	1.4	0.92	3.2	0.75	0.0	-	0.0	-	0.0	-	0	-
salmon	1+	12.8	0.77	13.9	0.69	0.07	-	0.2	-	2.8	0.77	9.5	0.63
	≥2+	11.4	0.74	5.9	0.72	0.6	-	0.2	-	13.4	0.61	22.0	0.56
	Total	25.6	-	23.0	-	0.7	-	0.4	-	16.2	-	31.5	-

	Physical characteristics					
	Pool	Riffle	Pool	Riffle	Pool	Riffle
Water velocity ($cm \cdot s^{-1}$)	0.17 ± 0.10	0.42 ± 0.15	0.16 ± 0.13	0.41 ± 0.12	0.12 ± 0.06	0.33 ± 0.13
Water depth (cm)	30.6 ± 8.1	18.6 ± 5.0	23.4 ± 9.7	15.0 ± 8.2	42.1 ± 7.7	16.4 ± 3.5

Table 2. Slope and mean intercept (mean ± SD) for self-thinning regressions in near allopatric (North Gunn Creek) and sympatric (South Gunn Creek and Chandler Creek) sites, by habitat type and sampling period (n = 3 sections for each sampling period and n = 9 sections for all periods combined in near allopatry; n = 6 sections for each sampling period and n = 18 sections for all combined period in sympatry).

Sampling period	Habitat	Near allopatry		Sympatry	
		Intercept	Slope	Intercept	Slope
June	pools	3.23 ± 0.03	-0.36 ± 0.16	2.26 ± 0.66	-0.04 ± 0.32
	riffles	3.36 ± 0.22	-0.57 ± 0.05	1.59 ± 0.61	-0.13 ± 0.18
July	pools	4.40 ± 0.29	-0.48 ± 0.23	2.32 ± 0.89	-0.05 ± 0.32
	riffles	3.95 ± 0.19	-0.95 ± 0.29	2.00 ± 0.99	-0.24 ± 0.31
August	pools	4.62 ± 0.26	-0.41 ± 0.20	2.95 ± 1.00	-0.26 ± 0.30
	riffles	4.63 ± 0.35	-1.14 ± 0.48	2.38 ± 1.10	-0.36 ± 0.48
All periods combined	pools	4.08 ± 0.68	-0.42 ± 0.18	2.51 ± 0.87	-0.12 ± 0.31
	riffles	3.98 ± 0.59	-0.88 ± 0.38	1.99 ± 0.93	-0.24 ± 0.34

Table 3. ANCOVA and MANCOVA results for the effects of habitat type and salmon density on the slopes and intercepts of the self-thinning relation, by sampling period (n = 18 sections per sampling period). ϕ (1 - Wilk's λ) represents the fraction of total variance accounted for by an effect in MANCOVA.

Sampling period	Analysis	Dependent variable	Habitat			Salmon			Habitat × Salmon		
			F	*P*	ϕ	*F*	*P*	ϕ	*F*	*P*	ϕ
June	ANCOVA	Slope	5.24	<0.05		39.38	<0.001		0.0003	0.99	
		Intercept	1.16	0.30		28.65	<0.001		1.64	0.22	
	MANCOVA	Slope and Intercept	7.35	<0.01	0.51	19.89	<0.001	0.74	1.40	0.28	0.18
July	ANCOVA	Slope	6.80	<0.05		15.76	<0.01		0.15	0.71	
		Intercept	0.06	0.81		15.03	<0.01		1.47	0.25	
	MANCOVA	Slope and Intercept	8.62	<0.05	0.55	8.17	<0.01	0.54	1.03	0.38	0.14
August	ANCOVA	Slope	3.98	0.06		5.50	<0.05		0.21	0.65	
		Intercept	0.05	0.82		7.03	<0.05		0.12	0.73	
	MANCOVA	Slope and Intercept	5.00	<0.05	0.42	3.42	<0.05	0.33	0.10	0.91	0.02

Figure captions

Fig. 1. Regressions of mean density (numbers per $100m^2$) on mean mass of fish (g) for the 18 stream sections, by habitat type and sampling period.

Fig. 2. Joint variation in the self-thinning slopes and intercepts, by sampling period. Large open squares: near allopatry in riffles; small open squares: sympatry in riffles; large black circles: near allopatry in pools; small black circles: sympatry in pools. The 18 points in each sampling period plot refer to the slope and intercept of self-thinning regressions in each of 18 studies sections (9 pools and 9 riffles). Arrows for habitat and salmon represent the directions along which effects are greatest for each factor. Relative arrow lengths reflect the fraction of total variance accounted for by each factor.

Fig. 3. Left: summary of the habitat effect on self-thinning regressions, at average salmon density, by sampling period. Black lines: pools; dotted lines: riffles. Right: summary of the effect of salmon density on self-thinning regressions, averaged across habitats, by sampling period. Black lines: low density of salmon (mean for North Gunn Creek); dashed lines: overall mean for salmon density; dotted lines: high density of salmon (mean for Chandler Creek).

Figure 1

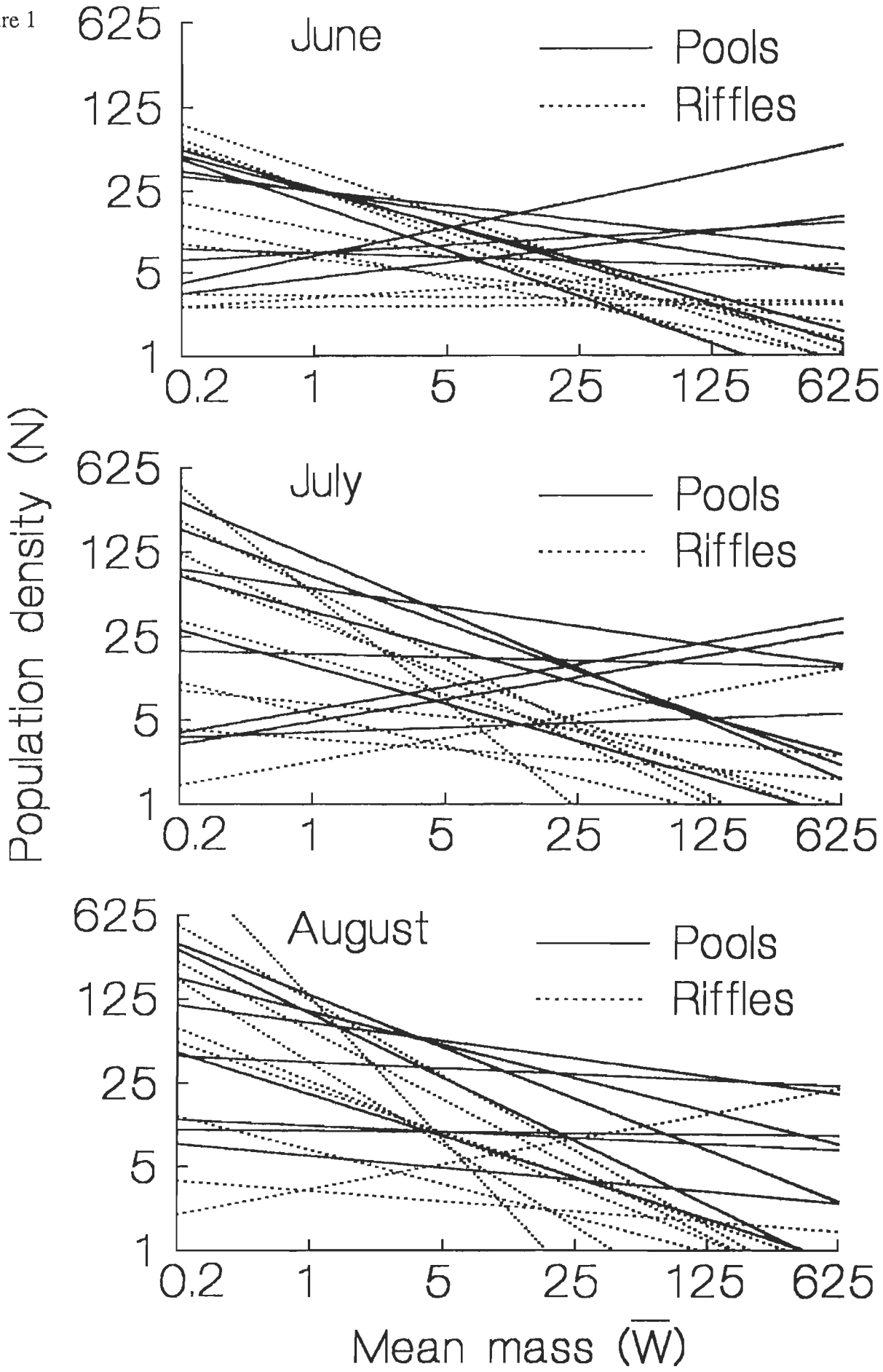

June
Pools
Riffles
625
125
25
5
1
0.2
1
5
25
125
625
July
Pools
Riffles
August
Pools
Riffles
Population density (N)
Mean mass (W)

Figure 2

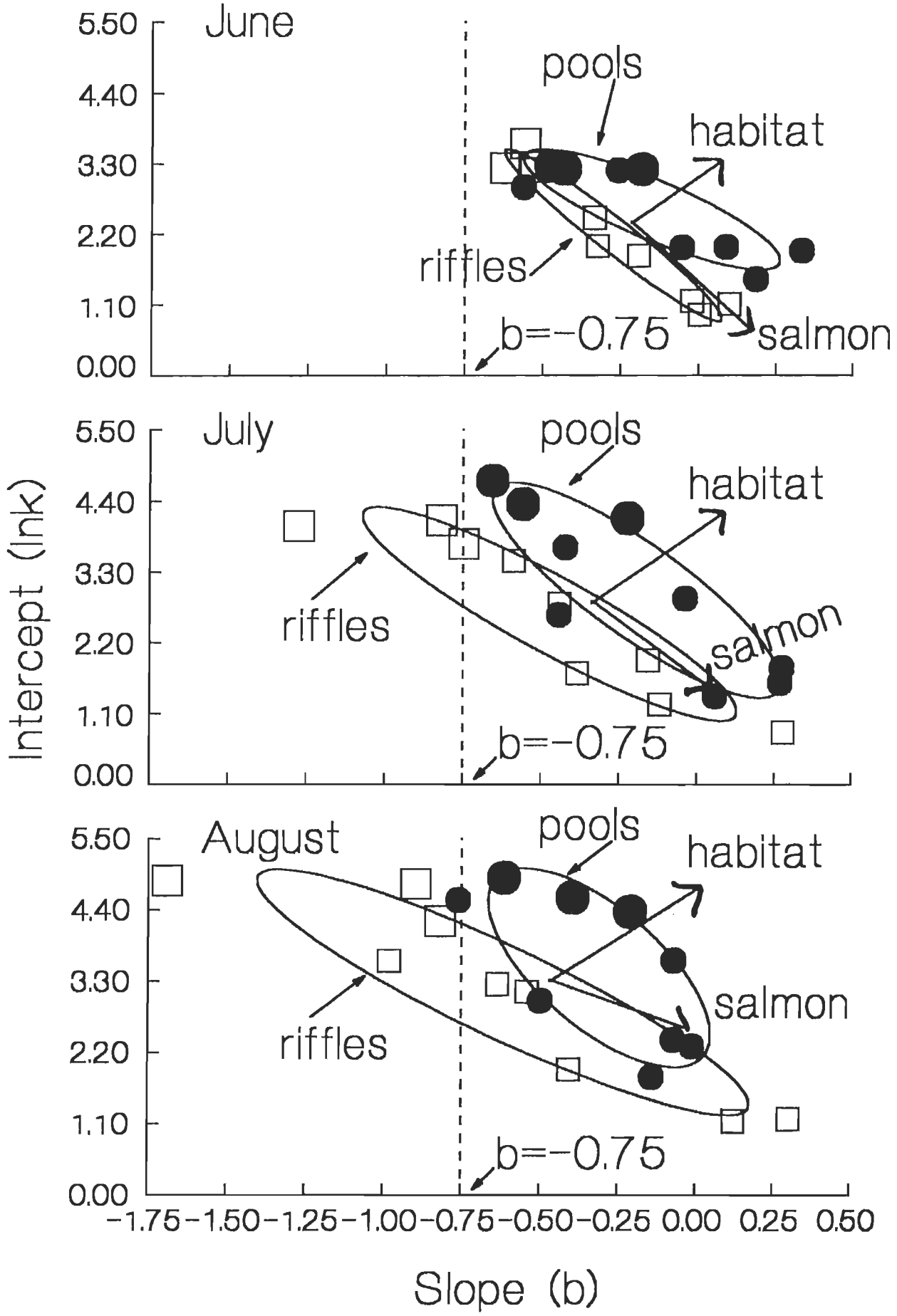
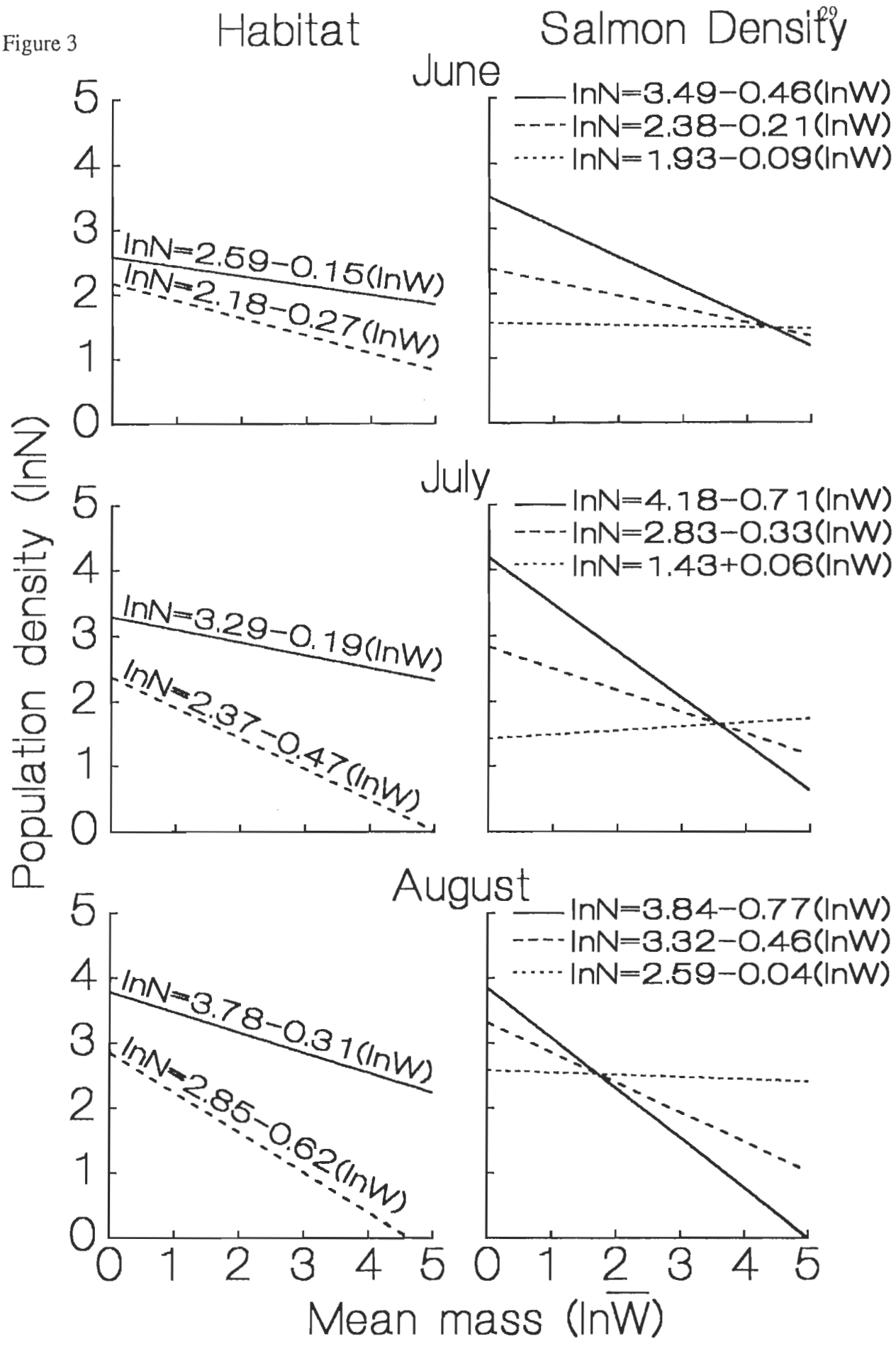

June
July
August
pools
habitat
riffles
salmon
b=-0.75
Intercept (lnk)
Slope (b)
5.50
4.40
3.30
2.20
1.10
0.00
-1.75 -1.50 -1.25 -1.00 -0.75 -0.50 -0.25 0.00 0.25 0.50

Figure 3


Habitat
Salmon Density
June
lnN=3.49−0.46(lnW)
lnN=2.38−0.21(lnW)
lnN=1.93−0.09(lnW)
lnN=2.59−0.15(lnW)
lnN=2.18−0.27(lnW)
July
lnN=4.18−0.71(lnW)
lnN=2.83−0.33(lnW)
lnN=1.43+0.06(lnW)
lnN=3.29−0.19(lnW)
lnN=2.37−0.47(lnW)
August
lnN=3.84−0.77(lnW)
lnN=3.32−0.46(lnW)
lnN=2.59−0.04(lnW)
lnN=3.78−0.31(lnW)
lnN=2.85−0.62(lnW)
Population density (lnN)
Mean mass (lnW)
0 1 2 3 4 5

CHAPITRE II

SELF-THINNING AND ANNUAL PRODUCTION IN STREAM SALMONIDS

Self-thinning and annual production in stream salmonids

by

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ABSTRACT

Conventional approaches to estimating annual production, such as Ricker's numerical method, usually require sampling fish populations on two or more occasions. In stream salmonids, a self-thinning equation often adequately describes the temporal trajectory of decline in individual numbers (per cohort) in relation to increase in mean individual weight. The equation therefore can be used to obtain a cross-sectional or snapshot view of production in the population. We used Ricker's method and a method based on integrating the area under the self-thinning curve to calculate annual production of brook trout, *Salvelinus fontinalis*, in streams of eastern Quebec, Canada. Production estimates obtained by the two methods were well correlated and were influenced similarly by various sources of variation: temporal variability, inter-habitat differences, and apparent effects of Atlantic salmon, *Salmo salar*. In salmonid populations that conform to the self-thinning relation, annual production can be estimated from point samples via the self-thinning relation. Because it reduces sampling effort, this approach may provide a useful alternative to conventional methods that require repeated sampling, particularly for comparative surveys of multiple sites across a large area.

Introduction

Production is defined as the quantity of tissue elaborated in a time interval, including that formed by individuals that do not survive to the end of this interval (Ivlev 1966). Commonly used methods for calculating annual production include numerical estimation based on specific models for growth and mortality (Ricker 1946), and graphical methods (Allen 1951). Ricker's numerical method uses exponential models of growth and mortality, with:

$$G = \frac{\ln \overline{W}_2 - \ln \overline{W}_1}{\Delta t} \tag{1}$$

$$Z = -\frac{\ln N_2 - \ln N_1}{\Delta t} \tag{2}$$

$$\overline{B} = \frac{B_1\left(e^{(G-Z)\Delta t} - 1\right)}{(G - Z)\Delta t} \tag{3}$$

$$P = G\overline{B}\Delta t \tag{4}$$

where G is the instantaneous rate of increase in weight; $\overline{W}_1$ and $\overline{W}_2$ are the mean weights of fish at times t_1 and t_2; Δt is the time interval between t_1 and t_2; Z is the instantaneous rate of mortality; N_1 and N_2 are the numbers of fish present at times t_1 and t_2; $\overline{B}$ is the mean biomass during Δt; B_1 is the biomass at time t_1; and P is the production during Δt (Chapman 1978). Equation 3 is used instead of a simple arithmetic mean of biomass between t_1 and t_2 when Δt refers to a long period of time, e.g., one year (Waters 1977).

In the Allen curve method, production estimates are obtained by plotting the number of individuals (N) in the population against the mean body mass ($\overline{W}$) of individuals at successive times and calculating the area under the curve that connects the points. Because no specific model of growth or survival is required for this method, an arbitrary choice must be made to determine how to interpolate between the estimates (Chapman 1978).

For salmonid fish, the self-thinning relation (Elliott 1993; Grant 1993; Bohlin et al. 1994):

$$D = k\overline{W}^{-b} \tag{5}$$

usually expressed as:

$$\log D = \log k - b \log \overline{W} \tag{6}$$

where D is population density and $\overline{W}$ is mean body mass, provides an explicit model of survivorship and growth that can be used to obtain estimates of annual production. This relationship describes how population density (D) decline (by mortality) as mean body mass ($\overline{W}$) increases (by individual growth). The value of the slope, b, for the self-thinning relation in salmonids had been the subject of much discussion. A slope of -1.00 is expected if a constant biomass can be supported by the habitat regardless of the size of individuals in the cohort (the biomass equivalence hypothesis; Begon et al. 1986, Grant 1993). The energetic equivalence hypothesis (Damuth 1987; Nee et al. 1991; Marquet et al. 1995) assumes that F, the total energy used by a population per unit area, is constant. Given that metabolic rate in animals is generally proportional to individual weight to the power of 0.75 (Kleiber 1961, Peters 1983), total energy use by the population should be proportional to (mean weight)$^{0.75}$ (eq. 2), and thus the slope of the self-thinning relation should be -0.75 (eq.3). In juvenile brown trout, *Salmo trutta*, populations, the slope of the self-thinning relation for cohorts followed over a 23-year period was remarkably close to -0.75 (Elliott 1993). Grant (1993),

using published data, found that three of four studies were consistent with a thinning line with a slope -0.75. However, Bohlin et al. (1994) stressed that the mean metabolic rate for salmonids was closer to 0.90 than to the value of 0.75 (Glass 1969) and showed that their estimate for the self-thinning slope (-0.98; 95% confidence interval -0.84 to -1.13), was not different from -0.90. Their reanalysis of data for juvenile Atlantic salmon in Shelligan Burn, Scotland (Egglishaw and Shackley 1977) yielded an estimate of -0.91 for the slope of self-thinning relation (Bohlin et al. 1994). A reanalysis of the relation between territory size and body size for stream salmonids (Grant and Kramer 1990) yielded a self-thinning slope of -0.86 (Bohlin et al. 1994).

For populations conforming to the self-thinning relation, annual production can therefore be estimated by integrating to obtain the area beneath the self-thinning curve:

$$P = k\int_{\overline{W}_i}^{\overline{W}_f} \overline{W}^{-b}\, dw \tag{7}$$

$$P = \frac{k}{1-b}\left(\overline{W}_f{}^{1-b} - \overline{W}_i{}^{1-b}\right) \tag{8}$$

where P is the estimate of annual production; k is the constant in eqs. (5) and (6); b is the slope of the self-thinning relation; $\overline{W}_f$ is the mean weight of individuals for the oldest age-class included in the analysis and $\overline{W}_i$ is the mean weight for the youngest age-class. In situations where the self-thinning relation accurately describes growth and mortality, it may be possible with this method to obtain estimates of annual production by sampling fish densities in a stream only once in summer. This method may be thus useful for comparing stream productivity in time and space (Bohlin et al. 1994), particularly when it is desirable to survey many sites.

The self-thinning method and conventional methods may differ in their ability to detect the effects of changes in environmental conditions (e.g., habitat type, density of potential competitors) on salmonid production. Physical differences between pools and riffles may lead to differences in growth or mortality rates between the two habitats, thus affecting production estimates. Interspecific competition with other salmonids has been shown to reduce the production of brook trout, Salvelinus fontinalis (Waters 1983; Whithworth and Strange 1983; Scarnecchia and Bergensen 1987). Competitive interactions with juvenile Atlantic salmon, *Salmo salar*, may affect brook trout production by influencing mortality or growth (Kennedy and Strange 1986, Gibson et al. 1993).

In this study, we estimate annual production for brook trout populations in streams of eastern Quebec using Ricker's numerical method and a method based on the self-thinning relation. We compare the production estimates obtained by these two methods, and examine whether physical (habitat type) and biological (potential interspecific competitors) aspects of the environment influence the two methods similarly.

Materials and methods

The three study sites, Chandler Creek (48º37' N, 67º06' W), North Gunn Creek (48º32' N, 67º07' W), and South Gunn Creek (48º32' N, 67º06' W) are located in the Matapedia Valley, eastern Quebec, Canada. Brook trout and Atlantic salmon are the dominant species at the study sites; slimy sculpin, Cottus cognatus, and longnose dace, Rhinichthys cataractae, are present also at low densities in Chandler Creek. At each site, fish were sampled in three short stream stretches consisting each of a pool section adjacent to a

riffle section (mean section length = 11.8 m). The distances between pool-riffle pairs were 14 and 225 m in Chandler Creek, 37 and 14 m in North Gunn Creek, and 29 and 33 m in South Gunn Creek. Section areas ranged from 25 to 186 m^2. Samples were collected three times during the summer (June 7-17, July 5-24, August 2-20) in 1993, 1994, and 1995. Each stream section was closed with modified seine net (6 mm mesh size) and fish were collected with a backpack electroshocker (Smith-Root model 15-C) in an upstream direction (3 to 6 passes). Fish were anesthetized with MS-222, measured to the nearest millimeter, and weighted to the nearest centigram. Fish densities (numbers per $100m^2$) were estimated separately for each species and age-class (removal method; Rexstead and Burnham 1991). Fish were assigned to age-classes 0+, 1+, and ≥ 2+ on the basis of length-frequency distributions, verified by examination of scales (Lacroix 1989).

Substrate type, stream depth, and stream wet width were measured along three (1993 and 1994) or five (1995) transects in each section at five equidistant points on each transect. Substrate type (index of coarseness on a scale from 1 to 12; modified from Bain et al. 1985) was evaluated within 30×30 cm squares centered at the sampling points. Stream velocity (cm s^{-1}) was measured at seven points on the central transect of each section with a pygmy-type current meter (Scientific Instruments model 1205). Discharge (m^3 s^{-1}) for each section was calculated from velocity and depth measures at the central transect. Maximum depth was measured at the deepest point in the section. Canopy opening, a measure of shading, was evaluated at the central point of each of three (1993 and 1994) or five (1995) transects with a forestry clinometer for each section. Conductivity (μS cm^{-1}) was measured in 1995 only. Environmental measures and fish densities are given in Table 1.

Annual production was estimated by Ricker's numerical method (Ricker 1946, Chapman 1978) for the intervals 1993 to 1994 and 1994 to 1995 (Δt = one year; eqs. 1 - 4). At each stream site, production was evaluated for the three pools combined and the three riffles combined (n = 36 estimates; 2 years, 3 summer periods, 3 study sites, and 2 habitat types), and for all six stream sections jointly (n = 18; 2 years, 3 summer periods, and 3 study sites). Separate estimates of annual production were calculated for the June, July, and August sampling periods. Production of the fry portion of the population up to each sampling date was estimated as in Randall and Chadwick (1986). Emergence was assumed to occur on 24 May for each year. A mean weight of 0.085 g was used for fry (Randall 1982). The density of fry at emergence was calculated as:

$$D_{adj.} = D_{obs.} e^{-Z\Delta t} \tag{9}$$

where $D_{adj.}$ is the density of emergent fry; $D_{obs.}$ is the density of 0+ fish at the sampling date in each year; Z is the instantaneous mortality rate estimated for survival of 0+ fish through 1+ the next year, and Δt is the number of days between emergence and the sampling date (Randall and Chadwick 1986). Annual production was the sum of production of three age-groups: emergent fry to 0+ at t_1, 0+ at t_1 to 1+ at t_2, and ≥1+ at t_1 to ≥ 2+ at t_2, where t_1 and t_2 are the beginning and the end of the yearly interval (Randall and Chadwick 1986, Bergheim and Hesthagen 1990). We obtained 18 production estimates for each yearly interval (3 summer periods, 3 stream sites, and 2 habitat types).

For each stream site, separate estimates of production were obtained by the self-thinning method (eq. 8) for the three pools combined and for the three riffles combined (n = 54 estimates; 3 years, 3 summer periods, 3 study sites, and 2 habitat types). Production estimates also were calculated for the three study sites (pools and riffles combined; n = 27

estimates; 3 years, 3 summer periods, and 3 stream sites). The slope and intercept of the self-thinning relation were obtained by model II (major axis) regression (Ricker 1973 1984, McArdle 1988, LaBarbera 1989). The initial weight used in eq. 3 ($\overline{W}_i$) was the weight of emergent fry (0.085 g, Randall 1982); the final weight ($\overline{W}_f$) was the geometric mean weight of all ≥ 2+ fish.

The effects of habitat type and salmon density on production estimates from the Ricker and self-thinning methods were examined by ANCOVA. Annual or interannual periods were analyzed separately: 1993 to 1994 and 1994 to 1995 for Ricker's method, and 1993, 1994, and 1995 for the self-thinning method.

Annual production calculated by the Ricker method was compare to production estimates for brook trout populations from the literature. Published estimates were selected for which a measurement of conductivity ($\mu S\ cm^{-1}$), an indicator of potential productivity, was also available.

Results

Previous studies have shown that production of brook trout populations is positively related to stream conductivity (O'Connor and Power 1976, Scarnecchia and Bergensen 1987, Waters et al. 1990). Chandler Creek and South Gunn Creek were below the regression line of production on conductivity, indicating low production in relation to stream potential (Fig. 1).

Overall, patterns of variation (temporal, between streams, and between habitats) in annual production were similar for the two methods (Fig. 2). Mean annual production was higher in pools than in riffles, for the three stream sites (Fig. 2). Production in North Gunn

Creek, where salmon were scarce, was higher than in the two other stream sites, where salmon had higher abundance (Fig. 2, Tables 2 and 3). Production estimates for both methods tended to increase over the summer, particularly so for North Gunn Creek (Fig. 2). Self-thinning estimates of production for 1994 and 1995 were well correlated with the average of Ricker estimates for 1993-1994 and 1994-1995 (Fig. 3). The relation between self-thinning estimates for 1993, which reflect production in years preceding 1993, had lower correlation with Ricker estimates for 1993 to 1995 (Fig. 3).

For both methods of estimation, production was markedly influenced by habitat type and by the density of Atlantic salmon, (Fig. 4, Table 3). At a given salmon density, production was higher in pools than in riffles (Fig. 4, Table 3). Production decreased with increasing salmon density for both methods of estimation (Fig. 4; Table 3).

Production of the fry to 1+ (previous to the second growing season) group seemed to be more strongly affected by the density of juvenile Atlantic salmon than was that of fish older than 1+ (Fig. 5). In North Gunn Creek, where salmon are scarce, fry and 0+ made up 45.4% of the total production in the population, but this percentage declined to 33.6% in the two other stream sites, where salmon are abundant (Fig. 5). Both age groups (fry to 1+ and ≥1+) showed decreased production when salmon density was high, but the fry to 1+ group showed the strongest decline in relation to production in allopatric stream sites (Fig. 5).

Discussion

In Ricker's method, both growth and mortality must follow an exponential model with parameters that remain constant or vary similarly over the study interval (Chapman 1978). Consequently, the time interval between samples is usually selected to be short

enough so that these assumptions can be reasonably expected to be valid; one month has generally been considered a satisfactory interval for fish (Waters 1977, Chapman 1978). Randall (1981) suggests a minimum of four surveys annually. If the above assumptions are held to be valid over a longer period of time, then little or no gain in statistical precision is realized by increasing the number of sampling dates (Newman and Martin 1983), and thus the sampling interval may be longer, e.g. one year for fish (Chapman 1978).

In the Allen curve method, normally the curve would be built by following the numbers and mean weight from the time of hatching through the entire life of a single cohort, until the last fish died. However, if between-year (or between-cohort) stability of populations can be assumed, a composite Allen curve representing each age group present can be built; the production of a single cohort will then be equal to the annual production of the mixed-age population (Chapman 1978). This procedure, applied originally by Allen (1951) to a brown trout population, has also been used for brook trout (Cooper and Scherer 1967, O'Connor and Power 1976).

The self-thinning method applies only in fish populations that have a discrete age-class distribution. It is critical that sufficient number of individuals be sampled in each age-class, especially for the oldest and youngest age classes used in determining $\overline{W}_f$ and $\overline{W}_i$.

Methods for estimating production yield erroneous estimates when there are large sampling errors and bias in population and survival estimates (Chapman 1978). Sampling biases in the removal method of population estimation can influence production estimates, but such biases can be assumed constant in comparisons across multiple sites for fishery management (Randall and Chadwick 1986). Although production estimates in this study were based on only one survey per year, results were comparable from year to year,

suggesting that estimates were precise. A similar conclusion applied to production estimates in the Matamek river, where results based on yearly surveys were comparable across years (O'Connor and Power 1976).

For most sites, production estimates increased over the summer. This trend can be attributed to the increases in numerical density which result from fish being concentrated in smaller areas as discharge declines seasonally. Production increases over the summer were greatest in North Gunn Creek, the site in which decline in discharge was strongest over the summer (Trépanier and Rodríguez., unpublished data).

Conductivity is considered a reliable indicator of biological productivity (McFadden and Cooper 1962, Cooper and Scherer 1967), which could be related to the supply of drift invertebrates (Waters 1977). Production estimates for North Gunn Creek, where brook trout are in near allopatry, were similar to those for fertile streams in earlier studies (Fig. 1). Although the two other stream sites in which trout are sympatric with salmon had high conductivity, they had production values comparable to those of infertile streams in the literature (Fig 1). In sympatry, the effect of juvenile Atlantic salmon on brook trout growth and mortality are strongest for trout in age-class 0+ (Gibson 1973; Gibson et al. 1993). Fish in the 0+ class typically account for a large proportion of the total production of a stream (e.g. 90% for three salmonid species, Shelligan Burn, Scotland; Egglishaw 1970). In the River Wye, England, 0+ and 1+ fish contributed 72% of the total annual production (Gee et al 1978). In our study, production of 0+ and 1+ fish ranged from 11.5 to 57.7% of total production (mean = 31.0%, n = 12 sites) in sympatric sites (South Gunn Creek and Chandler Creek). These estimates ranged from 36.1 to 86.7% (mean = 49.3%, n = 6 sites) in near allopatric sites (North Gunn Creek). In near allopatry, 0+ brook trout accounted for 74.3 %

of the total density of trout, but in sympatry this percentage declined to 59.8% in South Gunn Creek, and to 32.7% in Chandler Creek. A comparable decline in the proportion of 0+ brook trout was observed in the Matamek River, from 70% in near allopatry to less than 30% in sympatry with juvenile Atlantic salmon (Gibson 1973).

Production was higher in pools than in riffles both in near allopatry and sympatry. Available habitat volume is higher in pools, possibly allowing more trout territories to be maintained in this habitat (Grant and Kramer 1990). Brook trout may have access to a larger food base in pools than riffles, because prey items sink to the bottom more readily in the lower velocities characteristic of pools (McLay 1970). Brook trout in pools also tend to school instead of defending territories, which possibly allows more fish to be maintained per unit area than in riffles (Keenleyside 1962; Gibson 1978)

Production is often considered one of the most useful measures of the ecological success of a population (LeCren 1969; Hunt 1974; Waters 1977, 1992). Many fisheries managers maintain long-term yearly records of fish densities and weights (Waters, 1992); these data can be used to estimate production by the self-thinning method. In fish populations that conform to the self-thinning relation, annual production can be estimated from point samples via the self-thinning relation. Because it reduces sampling effort, this approach may provide a useful alternative to conventional methods that require repeated sampling, particularly for comparative surveys of multiple sites across a large area.

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References

(pages 61-71 à la fin du document pour les références de cet article)

Table 1. Physical characteristics and fish densities by stream site and by habitat type (mean values from 1993 to 1995 are given).

	Chandler Creek	North Gunn Creek	South Gunn Creek	Pools	Riffles
Mean depth (cm)	24.6	19.2	29.3	32.1	16.7
Maximum depth (cm)	52.4	44.1	61.0	71.0	33.6
Mean current velocity (cm s^{-1})	29.5	28.3	22.2	14.9	38.5
Mean discharge (m^3 s^{-1})	0.53	0.19	0.41	0.35	0.40
Mean width (m)	6.3	4.2	6.7	5.7	5.8
Substrate coarseness index	6.9	6.3	6.7	6.3	6.9
Canopy opening (degrees)	73	99	108	96	90
Temperature (°C)	15.4	15.1	14.3	15.3	14.6
Conductivity (µs cm^{-1})	262	180	173	205	205
Trout density (number per 100 m^2)	15.5	99.7	55.9	74.5	39.5
Salmon density (number per 100 m^2)	27.3	0.6	25.3	15.4	20.0

Table 2. Mean production estimates ($g \cdot m^{-2} \cdot yr^{-1}$) from Ricker's method for each stream site (pools and riffles confounded, n = 2 years for each sampling period and n = 12 estimates for all period combined).

Sampling period	North Gunn Creek	South Gunn Creek	Chandler Creek
June	2.19	1.42	1.01
July	4.68	1.92	1.14
August	9.99	2.27	1.13
All period combined	5.62	1.87	1.09
	(1.81 - 12.00)	(1.18 - 2.51)	(0.81 - 1.44)

Table 3. Mean production estimates, slopes, and intercepts from the self-thinning method for each stream sites (pools and riffles confounded, n = 3 estimates for each sampling period). Production range is shown in parentheses.

Stream site	Sampling period	Production ($g \cdot m^{-2} \cdot yr^{-1}$)	Slope	Intercept
North Gunn Creek	June	3.25 (2.15 - 5.43)	-0.48	3.32
	July	6.10 (5.29 - 7.20)	-0.73	4.32
	August	12.40 (7.40 - 17.12)	-0.64	4.70
South Gunn Creek	June	1.67 (1.36 - 2.12)	-0.14	2.31
	July	1.94 (1.78 - 2.03)	-0.39	2.96
	August	2.92 (2.75 - 3.14)	-0.69	3.75
Chandler Creek	June	1.73 (1.25 - 2.60)	0.06	1.54
	July	1.77 (1.26 - 2.07)	0.17	1.39
	August	2.33 (1.30 - 3.60)	0.06	1.55

Table 4. ANCOVA for the effects of habitat type and salmon density on the production estimates by Ricker's and self-thinning methods (n=18 sections for each time interval analysis).

		Habitat		Salmon density		Habitat × Salmon density	
Calculation method	Year	F	P	F	P	F	P
Ricker	93-94	21.30	<0.001	22.50	<0.001	0.09	0.769
	94-95	9.70	0.007	5.73	0.030	0.69	0.421
Self-thinning	93	8.30	0.011	12.20	0.003	0.02	0.880
	94	5.90	0.029	9.80	0.007	0.38	0.548
	95	3.15	0.096	4.18	0.059	0.20	0.664

Figure captions

Fig. 1. Relationship between annual production estimates and conductivity for brook trout. Vertical bars represent the range of estimates in each study. a, b, c, d, e, f, g: Scarnecchia and Bergensen 1987; h: Hunt 1966; i, j: Cooper and Scherer 1967; k: Neves and Pardue 1983; l, m, n, o: O'Connor and Power 1976. Values for North Gunn Creek (NG), South Gunn Creek (SG), and Chandler Creek (CH) are from the present study and represent production estimate from Ricker method calculated from all six sections combined in each stream sites. Production estimates from the present study were not used in the regression ($P<0.05$; $n = 15$; $r^2 = 0.42$).

Fig. 2. Comparison of Ricker and self-thinning production estimates by stream sites, habitat type and summer period. Black bars: June; dashed bars: July; open bars: August. The $\overline{W}_f$ used to estimate the outlying production value for Chandler Creek riffles in June 1993 was based on only one fish.

Fig 3. Comparison between Ricker's estimate (two-year average) and self-thinning estimates of annual production (1993 to 1995). The 1-to-1 line is represented. Circles: pools; squares: riffles.

Fig. 4. Effects of habitat type and salmon density on production estimates by Ricker and self-thinning methods. Black circles: pools; open squares: riffles.

Fig. 5. Comparison of production of 0+ and ≥ 1+ trout in near allopatry (squares) and sympatry with salmon (circles). For the two age groups, the mean production in near allopatry was calculated with results from North Gunn Creek; mean production in sympatry was calculated with results from South Gunn Creek and Chandler Creek. Values near the symbols are the percent abundance of each age group in near allopatry or sympatry. Values next to arrows show the percent decline of production for each age group.

Figure 1

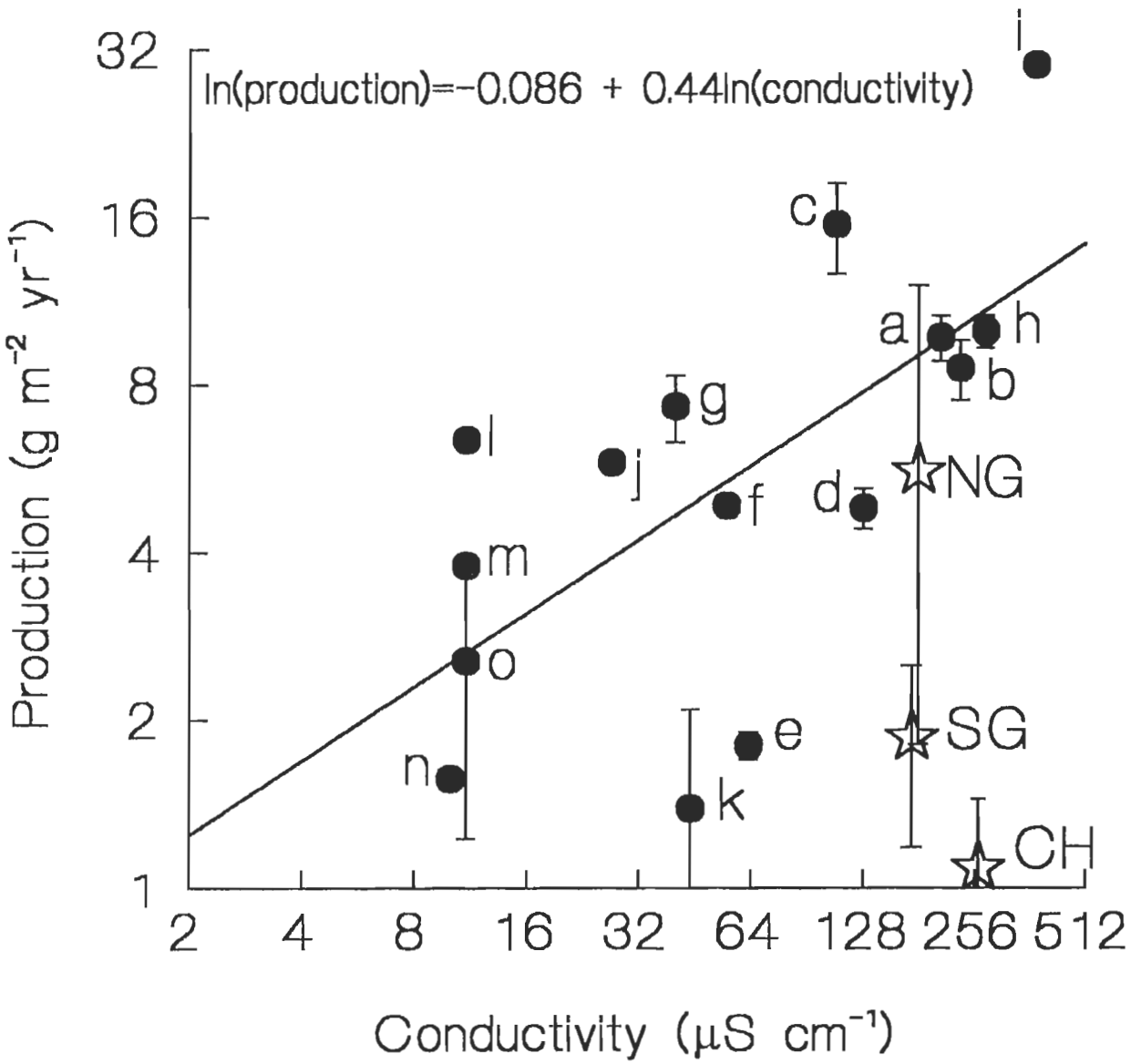

ln(production)=-0.086 + 0.44ln(conductivity)
Production (g m^{-2} yr^{-1})
Conductivity (µS cm^{-1})
32
16
8
4
2
1
2
4
8
16
32
64
128
256
512
a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
NG
SG
CH

Figure 2

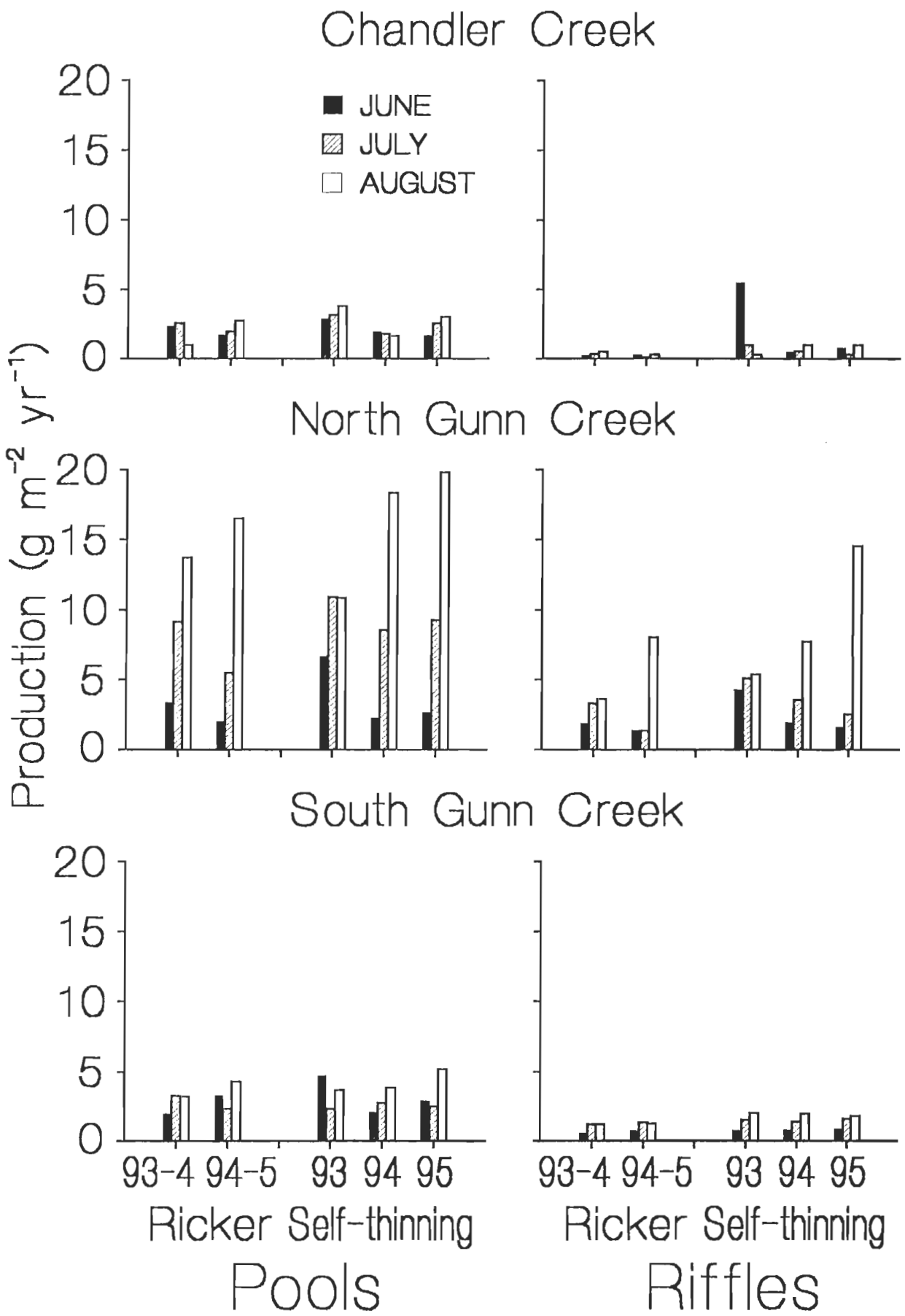

Chandler Creek
JUNE
JULY
AUGUST
North Gunn Creek
South Gunn Creek
Production (g m-2 yr-1)
20
15
10
5
0
93-4 94-5 93 94 95
Ricker Self-thinning
Pools
Riffles

Figure 3

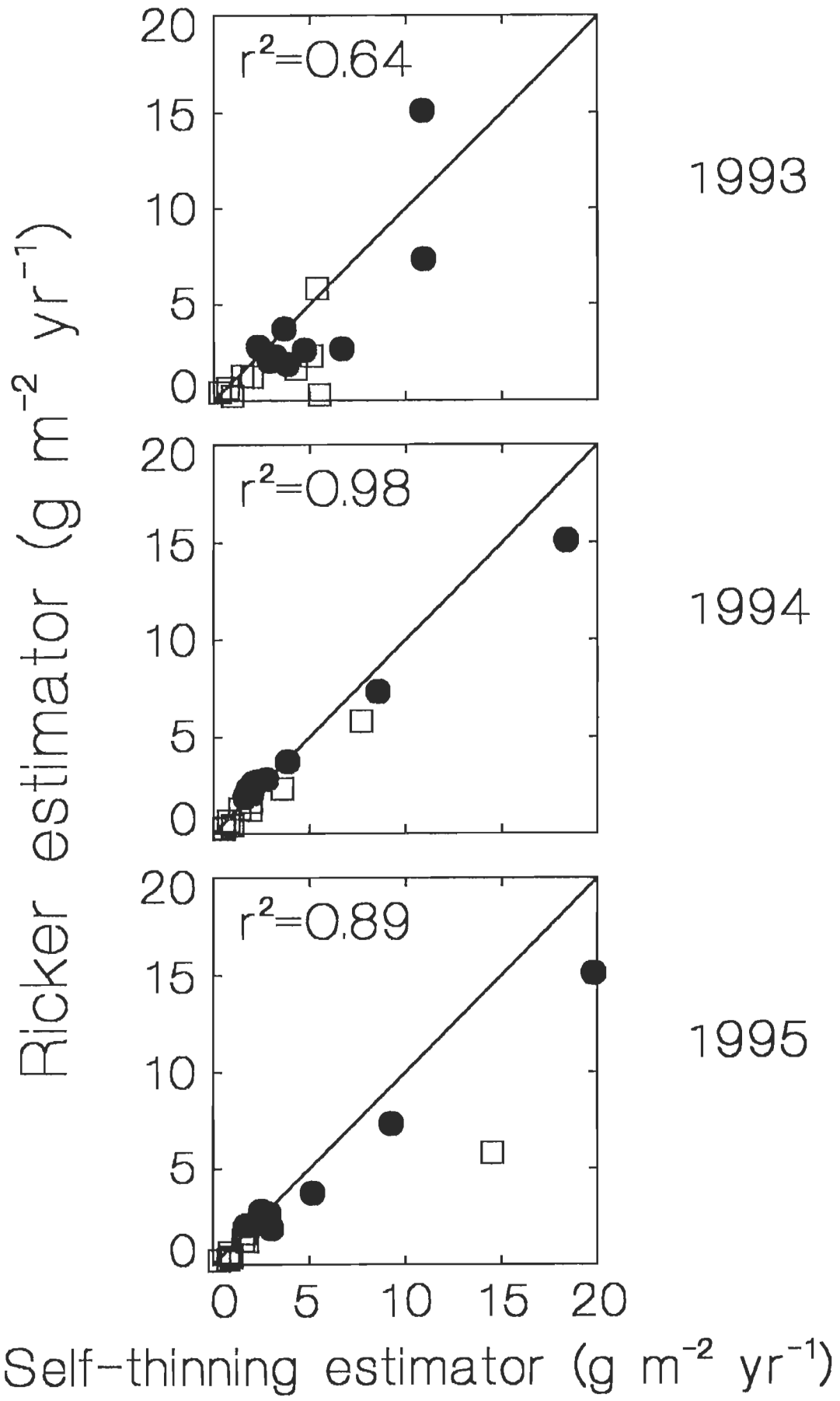

r²=0.64
r²=0.98
r²=0.89
1993
1994
1995
Ricker estimator (g m⁻² yr⁻¹)
Self-thinning estimator (g m⁻² yr⁻¹)
0
5
10
15
20

Figure 4

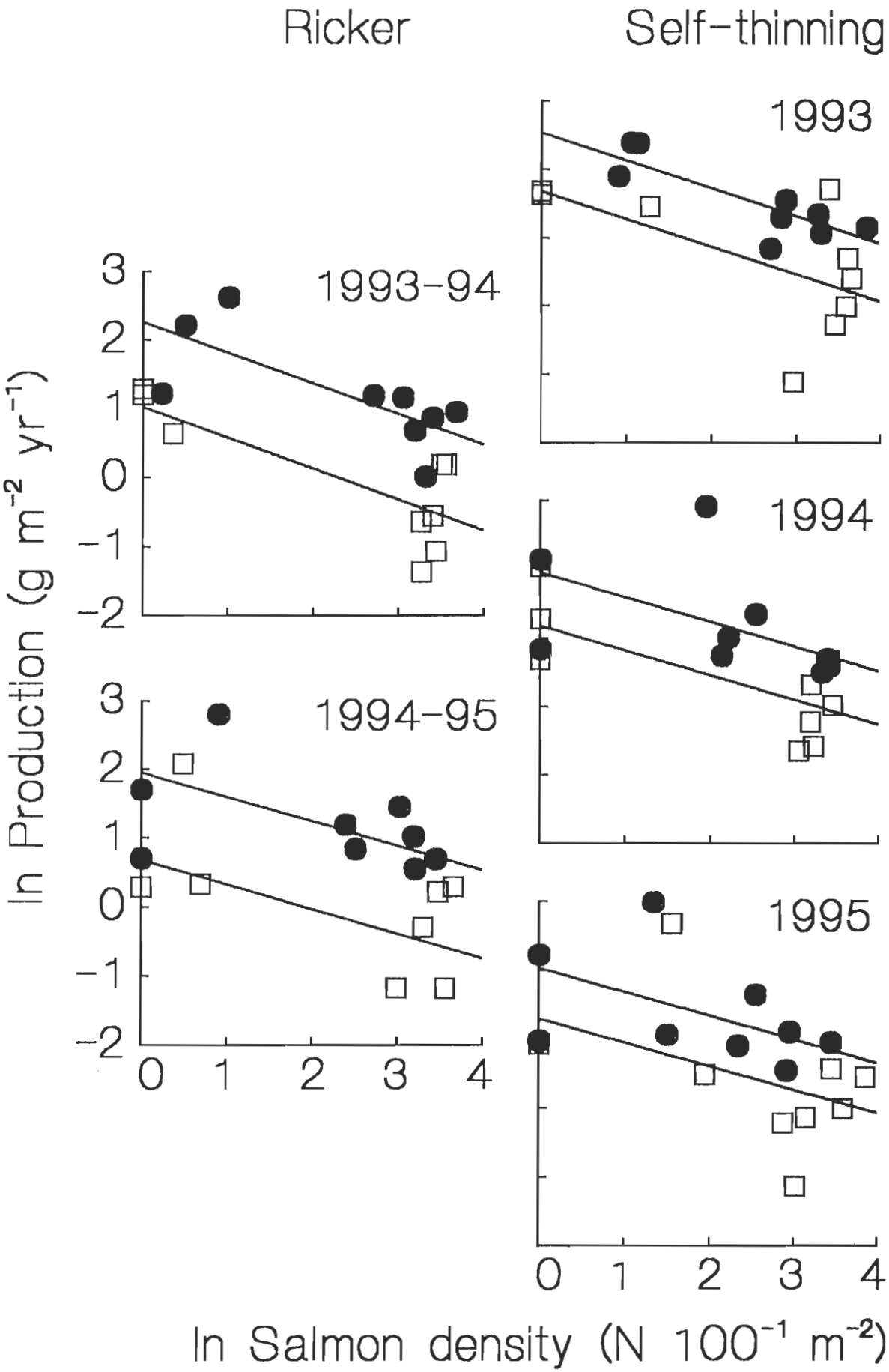
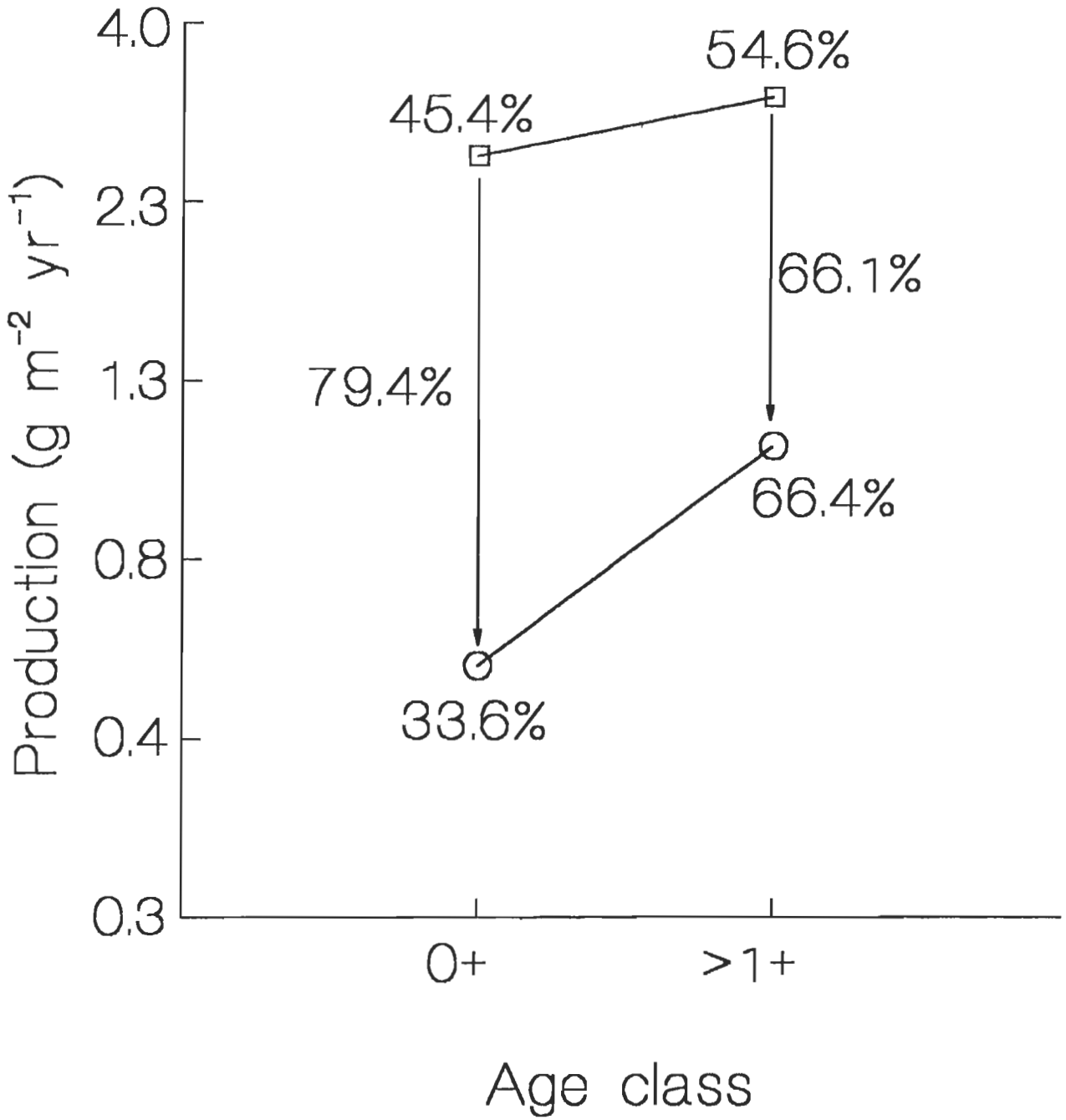

Ricker
Self-thinning
1993
1993-94
1994
1994-95
1995
ln Production (g m^{-2} yr^{-1})
ln Salmon density (N 100^{-1} m^{-2})
3
2
1
0
−1
−2
0
1
2
3
4

Figure 5


4.0
2.3
1.3
0.8
0.4
0.3
Production (g m^{-2} yr^{-1})
54.6%
45.4%
66.1%
79.4%
66.4%
33.6%
0+
>1+
Age class

CONCLUSIONS

Nous avons montré que la relation d'auto-éclaircissement pouvait avoir une pente de -0,90 , telle qu'attendu relativement aux considérations métaboliques, dans les rapides en situation allopatrique.

Nos résultats suggèrent par contre que même si la pente moyenne de la relation d'auto-éclaircissement est près de -0,90 dans les rapides en absence de compétiteurs interspécifiques, les pentes et ordonnées à l'origine peuvent varier dans d'autres habitats ou en présence de compétiteurs interspécifiques.

Dans nos sites d'étude, les pentes de la relation d'auto-éclaircissement pour les fosses étaient moins abruptes que celles dans les rapides, impliquant un rapport mortalité/croissance plus faible dans les fosses. Puisque notre système d'étude est ouvert, la mortalité ne peut être distinguée de l'émigration. Dans ce cas, les pentes plus abruptes dans les rapides pourraient résulter de perte d'individus par mortalité et par émigration combinées. Les pertes dans les rapides pourraient ainsi être dues principalement à des mouvements d'ombles plus gros des rapides vers les fosses.

Les pentes positives observées à des densités de saumons élevées dans les fosses ne peuvent résulter du processus d'auto-éclaircissement. Elles résultent probablement d'un apport de poissons plus gros à partir des rapides adjacents, couplé avec un déclin dans le nombre d'ombles plus jeunes causé par la compétition avec le saumon. Plusieurs études antérieures ont montré que les jeunes ombles étaient la classe d'âge la plus affectée par la

compétition interspécifique avec le saumon, et que les ombles se déplacent des rapides vers les fosses en vieillissant.

Les ordonnées à l'origine pour la relation d'auto-éclaircissement pour les fosses étaient plus élevées que dans les rapides, reflétant une capacité de soutien ou une biomasse plus grande dans les fosses. Le volume d'habitat disponible étant plus grand dans les fosses, il pourrait permettre le maintien d'un plus grand nombre de territoires. De plus, les ombles pourraient avoir accès à une ressource alimentaire plus grande, parce que les proies incluent dans la dérive sédimentent dans le fond des fosses dues à la plus faible vitesse de courant retrouvée dans cet habitat. Finalement les ombles tendent à se regrouper en banc dans les fosses au lieu de défendre des territoires, permettant une plus grande densité de poissons par unité de surface que dans les rapides. Ainsi, il semble qu'en sympatrie avec les juvéniles du saumon atlantique, les fosses soient de meilleurs habitats pour l'omble de fontaine que les rapides, une conclusion qui supporte les résultats d'études antérieures.

La densité des juvéniles du saumon atlantique avait pour effet d'abaisser l'ordonnée à l'origine et de rendre moins abrupte la pente de la relation d'auto-éclaircissement. Cette constatation reflétait une réduction générale des densités d'ombles sur toutes les classes-d'âge, avec un effet plus marqué sur les ombles plus jeunes et plus petits. Cette mortalité dépendante de la taille a été démontrée dans d'autres études sur la compétition entre l'omble de fontaine et les juvéniles du saumon atlantique en ruisseau.

Dans cette partie de l'étude, la relation d'auto-éclaircissement a apporté une représentation simple et interprétable de la dynamique des populations d'omble de fontaine, intégrant les effets de l'habitat et les interactions dépendantes de la taille des individus. La relation d'auto-éclaircissement pourrait ainsi être utile pour des comparaisons temporelles et

spatiales de productivité à l'intérieur et entre des ruisseaux contenant des ombles. Les études futures de la relation d'auto-éclaircissement devraient donc tenir compte des effets du type d'habitat et des compétiteurs présents.

Les méthodes utilisées couramment pour le calcul de la production annuelle, tel que la méthode numérique de Ricker et la méthode graphique de Allen, requièrent des échantillonnages successifs à l'intérieur d'une année afin d'obtenir des estimés de production représentatifs. Par contre, nos suggèrent que la méthode basée sur la relation d'auto-éclaircissement ne requiert qu'un seul échantillonnage estival par année.

Les estimés de production dans le ruisseau Gunn Nord, où les ombles sont en allopatrie, étaient similaires à ceux de ruisseaux fertiles dans la littérature. Les deux autres sites d'études où les ombles étaient en sympatrie avec les juvéniles du saumon atlantique, avaient une conductivité élevée malgré leur faible production, et étaient comparables à des estimés de production à l'intérieur de ruisseaux peu fertiles retrouvés dans la littérature.

Pour la plupart des sites à l'étude, les estimés de production augmentaient durant l'été. Cette tendance pourrait être attribuable à l'augmentation numérique de la densité, qui résulte de poissons qui se concentrent dans des aires plus restreintes lorsque le débit diminue en saison.

En situation de sympatrie, les ombles de la classe-d'âge 0+ étaient ceux dont la production était le plus fortement influencée par la compétition interspécifique. De façon générale, cette classe d'âge produit souvent entre 50 et 90 % de la production totale d'une population. Dans nos sites, la production de 0+ et de 1+ s'étendait de 11.5 à 57.7 % de la production totale (moyenne = 31.0 %, n = 12) dans les sites en sympatrie, et entre 36.1 et

86,7 % (moyenne = 49,3 %, n = 6) dans les sites allopatriques. Les effets dépendants de l'âge étaient reflétés dans les régressions d'auto-éclaircissement par une diminution de l'ordonnée à l'origine et une pente moins abrupte avec l'augmentation de la densité de saumons (voir point plus haut). Ces changements dans les pentes et ordonnées à l'origine réduisent l'aire sous la courbe de la relation d'auto-éclaircissement, et diminue ainsi la production annuelle à des densités de saumons plus élevées.

La production était plus élevée dans les fosses que dans les rapides, autant en allopatrie qu'en sympatrie. Le volume d'habitat disponible étant plus grand dans les fosses, il pourrait permettre le maintien d'un plus grand nombre de territoires. De plus, les ombles pourraient avoir accès à une ressource alimentaire plus grande, parce que les proies incluent dans la dérive sédimentent dans le fond des fosses dues à la plus faible vitesse de courant retrouvée dans cet habitat. Finalement les ombles tendent à se regrouper en banc dans les fosses au lieu de défendre des territoires, permettant une plus grande densité de poissons par unité de surface que dans les rapides. Ainsi, il semble qu'en sympatrie avec les juvéniles du saumon atlantique, les fosses soient de meilleurs habitats pour l'omble de fontaine que les rapides, une conclusion qui supporte les résultats d'études antérieures.

La production est considérée comme une des mesures les plus utiles du succès écologique d'une population. Plusieurs gestionnaires des pêches font des enregistrements annuels des poids et densités de poissons. Ces données pourraient être utilisées pour estimer la production par la méthode de la relation d'auto-éclaircissement. Chez les populations de poissons qui suivent la relation d'auto-éclaircissement, la production annuelle pourrait être évaluée à partir d'un échantillonnage unique en utilisant la relation d'auto-éclaircissement. Puisqu'elle réduit l'effort d'échantillonnage, cette approche pourrait s'avérer une alternative

utile aux méthodes conventionnelles qui requièrent des échantillonnages répétés, particulièrement pour des suivis comparatifs de sites multiples sur un grand nombre de cours d'eau.

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